ESTIMATING SUSTAINED YIELDS FOR MOOSE IN CENTRAL BRITISH COLUMBIA USING A PREDATOR-PREY MODEL

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ABSTRACT**:** One of the fundamental principles of wildlife harvesting is that it must result in a sustained yield (SY), a harvest that can be taken year after year without jeopardizing future harvests. Predator-prey models are rarely incorporated into estimates of SYs for moose, despite predation of moose by wolf (*Canis lupus*), grizzly bear (*Ursus arctos*), and black bear (*U. americanus*) throughout much of western North America. A simple predator-prey model was parameterized from a stable moose-wolf-bear system in central British Columbia during 1987–1998. Modelled moose, wolf, and harvest parameters compared favourably with observed parameters when the annual rate of wolf removal (human-caused wolf mortality) was 31%. SY curves were modelled by incrementally increasing wolf removal rates from 0 to 40% while maintaining selective moose harvests of 16% bulls, 2% cows and 9% calves. SYs displayed an S-shape curve with wolf removal rates, a hook-shape curve with wolf densities, and were linearly related to moose density. Optimal harvests included a moderate harvest of bulls (16–21%), a nil-to-very low harvest of cows (0–0.2%), and moderate-to-high harvests of calves (15–43%) when wolf removal rates were ≥ 20%. Higher cow harvest rates (2%) could be accommodated without substantially lowering SYs if calf harvest rates were reduced. Optimal harvest rates did not improve yields over bull-only hunting when wolf removal rates were 0–10% and management constraints were placed on adult sex ratios. This study supports previous findings that the optimal harvest strategy for moose should primarily target bulls and calves, whereas cows should be harvested minimally. However, for low-density, predator-limited moose populations, bull-only harvests may provide equivalent yields while maintaining higher moose and wolf densities.

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One of the fundamental principles of wildlife harvesting is that it must result in a sustained yield (SY), a harvest that can be taken year after year without jeopardizing future harvests (Sinclair et al. 2006). Caughley (1976) proposed a general model for harvesting ungulates that produces a yield-density curve with a bell-shape, slightly skewed to the right, and with the maximum sustained yield (MSY) occurring at ~ 70% of carrying capacity (K). Crête (1987) expanded on Caughley's model and proposed two yield-density curves for moose (*Alces alces*), one with wolves (*Canis lupus*) and bears (*Ursus* spp.) present (predator-limited K = 400 moose/1000 km^2), and the other without predators (food-limited K = 1000–2000 moose/1000 km^2). The predator-limited curve implied that lowering moose density to 200–300 moose/1000 km^2 through hunting will increase SYs about 4-fold. That is, by intensively harvesting moose, wolf numbers and predation rates should decline, and moose growth rates and harvest should increase. Gasaway et al. (1992) rejected the concept of a bell-shaped yield-density curve for moose in the presence of wolves and bears in Alaska and Yukon, and presented an approximate SY curve for moose where sustainable harvests increased more gradually with moose density. Their empirical data suggested that wolves and bears remained effective predators on calves at very low densities, and that SYs were lower than predicted by Crête's (1987) predator-limited, yield-density curve. Gasaway et al. (1992) concluded that predation by lightly harvested wolf, grizzly bear (*U. arctos*), and black bear (*U. americanus*) populations in Alaska and Yukon lowered and maintained moose populations within a low density dynamic equilibrium (LDDE, $\leq$ 417 moose/1000 km^2), and that intensive harvesting of predators, rather than moose, was required to elevate SYs. Hatter (1999) developed a preliminary yield-density curve for moose in north-central British Columbia (BC) that was similar in shape to the yield-density curve for Alaska and Yukon (Gasaway et al. 1992), suggesting that some moose populations in BC may also exist within a LDDE.

Although moose are limited by wolf and bear predation throughout much of North America (Bergerud et al. 1983, Gasaway et al. 1983, 1992, Crête 1987, Messier 1994, Van Ballenberghe and Ballard 1994), predator-prey models are rarely used in determining SYs for moose. Van Ballenberghe and Dart (1982) used a simple conceptual model to examine harvest yields subject to wolf and bear predation and found that bull-only hunts provided an equivalent numerical yield to either-sex hunts, but had a much higher margin of safety for management errors. More recently, attention has been given to optimizing SYs, or obtaining the maximum yield by selectively harvesting bulls, cows, and calves at different rates. Sæther et al. (2001) concluded that the optimal harvest strategy in northern Norway with few large predators, but within a fluctuating environment, involved a high harvest of calves and bulls, and that cows should hardly be harvested. Nilsen et al. (2005) considered moose populations in south-eastern Norway where due to strict management control there was no numerical response by wolves, and found that in the presence or absence of predation, a high proportion of calves in the harvest gave the highest SYs. Xu and Boyce (2010) considered moose populations in central Alberta subject to predation and stochastic weather events, and also concluded that when optimizing total yield, bulls and calves should be subject to intense harvest, with a low harvest of females. While the effect of predators on SYs was considered by Nilsen et al. (2005) and Xu and Boyce (2010), neither study modelled predator-prey dynamics in detail. The purpose of this study was to develop a model that explicitly considered predator-prey interactions over a range of fall wolf densities, and to use the model to investigate how predation affects SYs and optimal harvesting of moose in central BC. I considered the optimal harvest to be the highest sustained yield of moose from all sex/age classes, as opposed to the greatest carcass weight or maximizing hunting opportunity.

STUDY AREA

The 19,000 km^2 study area, hereafter referred to as the Prince George study area (PGSA), was located around Prince George (53° 54'N × 122° 41'W) in central BC (Fig. 1). The terrain is flat to rolling and forests are mainly hybrid white-Engelmann spruce (*Picea glauca x engelmannii*) and subalpine fir (*Abies lasiocarpa*) with extensive successional stands of lodgepole pine (*Pinus contorta*). Forestry is a prominent industrial activity and cutblocks are common throughout the area. Moose were probably the

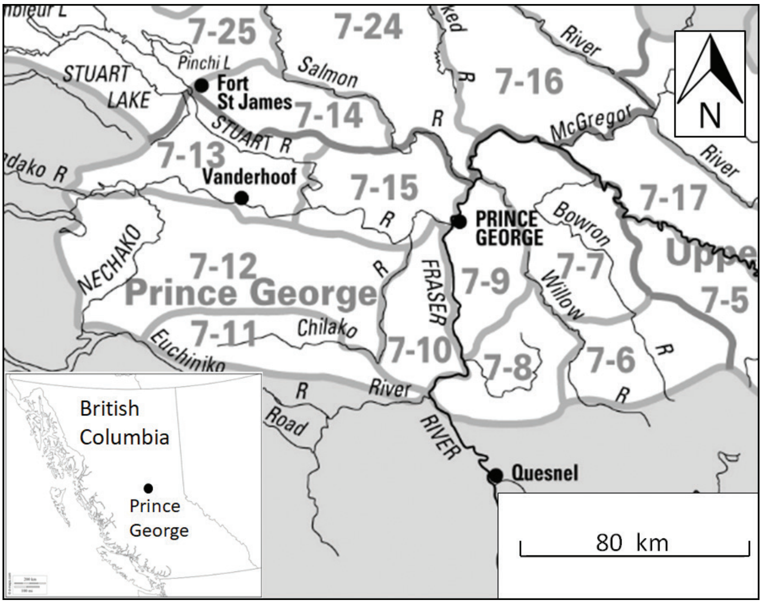

Fig. 1. Location of the Prince George study area (PGSA) in central British Columbia, Canada. The PGSA includes all of Wildlife Management Units (MU) 707–715, and the lower portions of 716 and 724.

predominant ungulate prey for wolves, black bears, and grizzly bears because other ungulates were rare, but included mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), elk (*Cervus canadensis*), and caribou (*Rangifer tarandus*) (Heard et al. 1999). The moose density estimated in 1998 was 1320 moose/1000 km^2 from a stratified random block survey when predator densities were ~12.5 wolves/1000 km^2, 20 grizzly bears/1000 km^2, and 211 black bears/1000 km^2 (Heard et al. 1999). Since 1980, selective fall harvests have governed moose hunting through a combination of differential licencing for bulls and cows and open seasons on 2-point bulls and calves (Child 1983). From 1991 to 1998, licenced hunters harvested an average of 16% of the bulls, 2% of cows, and 9% of calves for a harvest rate of 7% of the pre-hunt population (Heard et al. 1999). The First Nations harvest was unknown, but likely less than the licenced harvest (Heard, pers. comm.). Moose densities and composition, harvests, and hunter success rates appeared to be relatively stable from 1987 to 1998. There was no trend in the number of wolves shot by licensed hunters or Conservation Officers during this period implying that wolf densities were also stable. Heard et al. (1999) suggested that the elevated moose density was possible because wolf removals (human-caused wolf mortality) were high due to the combined effects of hunting, trapping, and killing wolves to protect livestock. Grizzly bears were lightly hunted and black bears appeared to be moderately exploited (Heard et al. 1997). Further details of the PGSA are provided by Heard et al. (1997, 1999).

METHODS

Model structure

Moose

The population was stage-structured as bulls (≥ 1 year-old males), cows (≥ 1 year-old females), and calves (< 1year-old with 50:50 sex ratio). Density dependence in reproduction and survival were modelled followed the approach outlined by McNay and Delong (1998) and ranged from 51 to 85 calves/100 cows at birth, 15–39% summer calf mortality, 10–12% winter calf mortality, 2–12% winter cow mortality, and 4–12% winter bull mortality. All density dependent responses started at ~ 65% of *K* and generally increased in a linear manner; *K* was set to 2000 moose/1000 km^2 (Crête 1987, Heard et al. 1999). Summer adult mortality (2%) was assumed to be density independent. The modelled population was censused 3 times per year including the post-hunt, post-calving, and pre-hunt periods. Wounding loss was set to 15% of the licenced harvest (Kuzyk et al. 2018). First Nations harvest was assumed to be unselective and occur during winter. The maximum harvest rate by First Nations was presumed to be 7% of the post-hunt moose population at *K*, declining linearly to 0% at 100 moose/1000 km^2. Where not specified, harvest rates were based on the pre-hunt moose numbers, while moose densities and sex-age composition apply to the post-hunt period.

Wolves

Changes in wolf density were modelled as a ratio-dependent numerical response:

$$W_t = W_{t-1} + rW_{t-1}\left(1 - \frac{W_{t-1}}{aM_{t-1}}\right)$$

(Eberhardt 1997, Hatter 2019) where W_t denotes fall wolf density at time t, r is the maximal rate of increase for wolves (r = 0.46, Keith 1983), a is the equilibrium ratio of wolves:moose, and M_t is moose density. Eberhardt et al. (2003) estimated $a = 0.049$ by linear regression of the observed finite rate of increase of wolves (λ) against the wolf:moose ratio. I added 6 additional data points (Appendix 1) and estimated the relationship as:

$$y = 1.534e^{-10.72x}$$

where y is the observed λ for wolves, x is wolves/moose, and a = 0.040 (25 moose/wolf, 95% CI: 20–29) when $y = 1.0$. Spring wolf numbers were estimated by subtracting the annual wolf removal from the fall population. The wolf removal rate included all human-caused mortality.

Several models have been proposed for estimating the annual kill rate of moose by wolves. Messier (1994) found that winter kill rates were reduced at low moose densities, and proposed a Type II functional response. Hayes and Harestad (2000) modified the parameter estimates for the Type II functional response based on kill rates from the Yukon, while Eberhardt (1997) suggested kill rates were density independent and averaged 2.1 kills/wolf/100 days in winter. Lake et al. (2013) concluded that kill rates were also density independent in Alaska and Yukon. Serrouya et al. (2015), however, found that Messier's Type II response provided the best fit among competing models for a wolf-moose-caribou system in south-eastern BC. I used Messier's (1994) functional response:

$$y = \frac{3.36x}{0.46 + x}$$

where y is the number of moose killed per wolf per 100 days in winter, and x is the number of moose/km^2, but capped the maximum killing rate at 2.1 as suggested by Eberhardt (1997). Following Eberhardt (1997), I assumed that summer kill rates were 75% of the winter rate during 5 months of summer (June–October). I used fall wolf densities for winter predation and spring wolf densities for summer predation. Wolf kills were apportioned among the bulls, cows, and calves by assuming the relative vulnerability of calves was 10-fold greater than adults during summer and 2-fold greater during winter. The high calf vulnerability reflected the preference by wolves for calves (Peterson et al. 1984, Sand et al. 2008). Calculations for relative vulnerability followed McNay and Delong (1998).

Bears

Ballard (1992) reported that calf mortality rates due to grizzly bear predation ranged from 3 to 52% and predation rates were independent of moose density; mortality rates from black bears predation ranged from 2 to 50%. The predation rates of grizzly and black bears on moose calves in the PGSA were unknown. Rea et al. (2019) found that only 2% of bear scats collected in the PGSA during spring and summer (n = 1381) contained moose calf hair; however, they noted that even this low percentage could result in substantial calf mortality. I assumed a combined annual calf predation rate by grizzly and black bears of 35%, that predation was density independent, and that these kill rates were additive to other forms of mortality. Adult grizzly bears have been reported to kill an average of 0.5–2.2 adult moose annually (Dahle et al. 2013), while black bears rarely kill adult moose (Ballad 1992). I assumed that the modelled 2% summer mortality rate for adults included kills by bears. I did not consider the effects of bear hunting on moose population dynamics as it would have made the model more complex and further increased uncertainty in the model projections.

Model evaluation

I evaluated the model by assessing how well the modelled moose and wolf parameters compared to the observed parameters in the PGSA when 16% bulls, 2% cows, and 9% calves were harvested annually. Model fitting was primarily achieved by adjusting the wolf removal rate until the modelled parameters closely matched the observed parameters. I ran each simulation for 100 years to remove transient predator-prey dynamics and to ensure that moose, wolf, and harvest densities were stable. I also compared modelled estimates of moose calf mortality rates and total annual mortality rates with those from field studies in Alaska and Yukon summarized by Boertje et al. (2009). Additionally, I tested for consistency between modelled estimates of wolf density with low removal rates (0–15%) and those generated from a prey biomass regression model, where wolf densities were estimated from an ungulate biomass index at the regional level in BC (Kuzyk and Hatter 2014).

As calf predation rates by bears were unknown, but could be substantial, I evaluated the sensitivity of different predation rates on the modelled parameters. I considered bear predation rates ranging from 10 to 50% in increments of 5%. For each predation rate, I used the optimization tool SOLVER in Microsoft Excel (Microsoft, Redmond, Washington, USA) to minimize the sums of squared differences between the observed and modelled parameters (Hilborn and Mangel 1997) by iteratively changing the wolf removal rate. The adjusted parameters included moose density, wolf density, moose harvest density, and moose sex:age ratios.

Sustained yield curve

SYs for moose in the PGSA were simulated by increasing annual wolf removal rates from 0 to 40% in increments of 1% while maintaining constant moose harvest rates for bulls (16%), cows (2%), and calves (9%). The SY was the moose harvest in the 100th year of the simulation. SY curves were generated for harvest density and wolf removal rates, harvest density and wolf density, and harvest density and moose density.

I evaluated the modelled yield-density curve by comparing it to the yield-density curve developed by Hatter (1999) for stable moose populations in north-central BC.

Optimal harvests

Optimal harvests were determined by iteratively changing the harvest rate for bulls, cows, and calves with SOLVER until the maximum total harvest was achieved, and moose and wolf populations were stable. A similar procedure was used for optimizing bull and calf harvests with cows harvested at 2%, and for bull harvests with cows and calves unharvested. Crête et al. (1981) recommended that in order to optimize moose harvest in south-western Quebec, at least 40% bulls should be retained among adults to ensure that sex ratio-dependent fertilization was not adversely affected. The provincial moose harvest management procedure for BC (FLNRO 2013) states that the lower range of the post-hunt adult sex ratio should not fall below 30 bulls:100 cows, or 50 bulls:100 cows in low density (≤ 200/1000 km^2) moose populations. Therefore, I added a sex ratio constraint when optimizing moose harvests with Solver to ensure the adult sex ratio was maintained at either ≥ 30 bulls:100 cows or ≥ 50 bulls:100 cows depending on moose density.

RESULTS

The modelled moose population, in the absence of hunting or predation, stabilized at 2000 moose/1000 km^2, with 100 bulls/100 cows and 32 calves/100 cows (Table 1). The finite rate of increase below population levels where density dependent effects became operative was $\lambda \sim 1.3$. The stable moose density was 9% lower with bears only (wolves and hunting absent), and 72% lower with wolves only (bears and hunting absent). With wolves and bears (no hunting), the stabilizing density was almost 90% lower, and consisted of 87 bulls/100 cows and 35 calves/100 cows.

The estimated parameters from the predator-prey model compared favourably with the observed parameters for the PGSA during the study period when the wolf removal rate was 31%. Both the modelled and observed wolf densities were 12.5 wolves/1000 km^2. The modelled moose density was 1310/1000 km^2 (observed: 1320/1000 km^2) and the harvest density was 100/1000 km^2 (observed: 99/1000 km^2), or 7% of the pre-hunt moose density = 99/(99+1320). The modelled adult sex ratio (40 bulls:100 cows) was lower than the observed ratio (46 bulls:100 cows), while calf:cow ratios were similar (modelled = 38 calves:100 cows, observed = 41 calves:100 cows). The modelled and observed moose:wolf ratios were the same (105:1).

Modelled summer moose calf mortality rates from wolves and bears, as well as total mortality rates, fell within the range reported from studies in Alaska and Yukon (Table 2a). The combined predation rates from wolves

Table 1. Comparison of modelled moose density, bull:cow ratios and calf:cow ratios for the PGSA without hunting or predation, with bear predation only, wolf predation only, and wolf and bear predation, central British Columbia, Canada.

Treatment	Moose/1000 km^2	Bulls:100 cows	Calves:100 cows
No hunting or predation	2000	100	32
Bear predation only	1828	100	22
Wolf predation only	567	90	58
Wolf and bear predation	218	87	35

Table 2. Comparison of modelled moose mortality rates for the PGSA in central British Columbia, Canada with studies in Alaska, USA and Yukon, Canada. Harvest rates were 16% bulls, 2% cows, and 9% calves.

a. **Summer mortality rates (%) on calves.**

Area, treatment	Wolves	Bears	Predation	Other	Total
PGSA, 30% wolf removal	3	35	38	15	53
PGSA, 20% wolf removal	5	35	40	15	55
PGSA, 10% wolf removal	6	35	41	15	56
Alaska/Yukon, min.[1]	*2*	*25*	*45*	*2*	*47*
Alaska/Yukon, max.[1]	*25*	*67*	*72*	*15*	*80*

[1] minimum (min.) and maximum (max.) estimates of collared moose calves killed among 8 radiotelemetry studies in Alaska and Yukon (from Boertje et al. 2009).

b. Annual mortality rates (%) on total post-calving moose population.[1]

Area, Treatment	Wolves	Bears	Other	Hunting	Total
PGSA, 30% wolf removal	5	13	10	9	37
PGSA, 20% wolf removal	7	13	10	7	37
PGSA, 10% wolf removal	8	13	10	7	37
Alaska/Yukon, min.[2]	*8*	*9*	*1*	*2*	*27*
Alaska/Yukon, max.[2]	*15*	*27*	*6*	*6*	*47*

[1] The annual mortality rate of the post-calving population = no. of moose deaths (including calves)/number of moose alive after all calves were born.

[2] Minimum (min.) and maximum (max.) estimates of annual predation rates and mortality rates among 4 post-calving moose populations during radiotelemetry studies in Alaska and Yukon (from Boertje et al. 2009).

and bears, however, were slightly lower. Annual wolf and bear predation rates on the post-calving population, as well as the total mortality rate, also fell within the range from Alaska and Yukon (Table 2b). Modelled estimates of wolf density with wolf removal rates ≤ 15% ($\bar{x}$ = 7 wolves/1000 km^2, range = 6–7) were similar to those from the ungulate biomass regression ($\bar{x}$ = 6 wolves/1000 km^2, range = 5–8).

The modelled parameters were sensitive to different bear predation rates on moose calves (Table 3). Moose densities, wolf densities, sex/age ratios, and moose harvests declined as bear predation rates increased. Wolf removal rates and the moose:wolf ratio increased as bear predation rates increased. SYs varied from 94 moose/1000 km^2 with 50% bear predation to 119 moose/1000 km^2 with 10% bear predation.

SYs for moose displayed an S-shape curve with increasing wolf removal rates (Fig. 2a). SYs gradually increased when wolf removal rates rose from 0 to 15%, while removal rates between 27 and 32% greatly increased SYs; removal rates > 31% only slightly increased SYs. Wolves sustained removal rates up to 31%, declined rapidly when removals were 31–38%, and were eliminated with 40% annual removal (Fig. 2b). SYs for moose based on wolf densities displayed a hook-shape curve (Fig. 2c). Wolf densities were 6/1000 km^2 when wolf removals were 0%. Moose densities (154/1000 km^2) and harvest densities (12/1000 km^2) were also low at this wolf density. As wolf removal rates increased, moose numbers and harvest also increased. Wolves responded to the moose increase due to the ratio dependent numerical response, and wolf densities rose until removal rates

Table 3. Sensitivity analysis of different bear predation rates on modelled wolf, moose and harvest parameters for the PGSA in central British Columbia, Canada. Harvest rates were 16% bulls, 2% cows and 9% calves. The sums of squares fit is the minimum sum of squared differences between the observed and modelled moose density, wolf density, harvest density, and bull:cow and calf:cow ratios.

Bear predation rate (%)	10	15	20	25	30	35	40	45	50
Wolf removal rate (%)	21	23	25	27	29	31	33	35	37
Moose harvest rate (%)	8	8	8	7	7	7	7	7	7
Harvest/1000 km^2	119	117	116	115	103	101	99	97	94
Wolves/1000 km^2	31	28	24	21	16	12	9	6	2
Moose/1000 km^2	1400	1400	1400	1400	1319	1319	1319	1320	1320
Moose/wolf	45	51	57	67	84	106	145	238	711
Bulls/100 cows	49	48	47	46	41	40	38	36	34
Calves/100 cows	60	56	53	49	41	38	34	31	28
Sums of squares fit	*7817*	*7526*	*7271*	*7061*	*156*	*136*	*171*	*269*	*441*

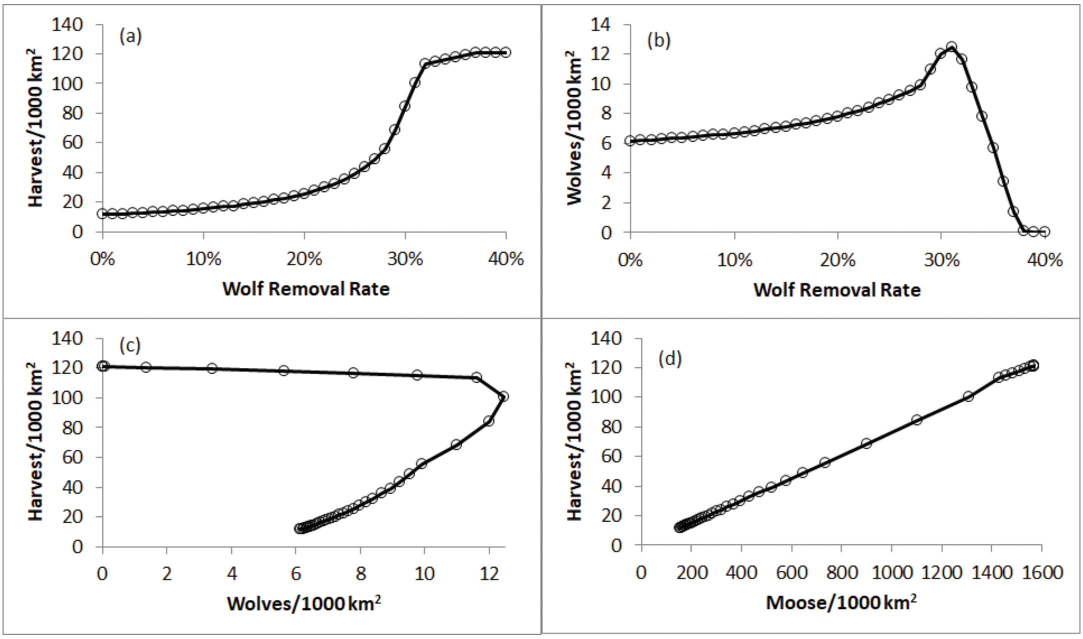

Fig. 2. Relationship between modelled moose and wolf parameters and SYs (moose harvest density) for the PGSA in central British Columbia, Canada with annual harvests of 16% bulls, 2% cows and 9% calves. Each data point (open circle) was generated by modelling predator-prey dynamics for 100 years with wolf removal rates ranging from 0 to 40%. (a) relationship between SYs and wolf removal rate; (b) relationship between wolf density and wolf removal rate; (c) relationship between SYs and wolf density; and (d) SY (yield-density) curve for moose harvest density and moose density.

reached 31%. Wolves were not able to compensate for removal rates above 31% and densities declined. Moose densities and harvest continued to increase as wolf densities declined, but at a much slower rate due to density dependent declines in moose reproduction and survival. Although wolf densities from 6 to 12/1000 km^2 were

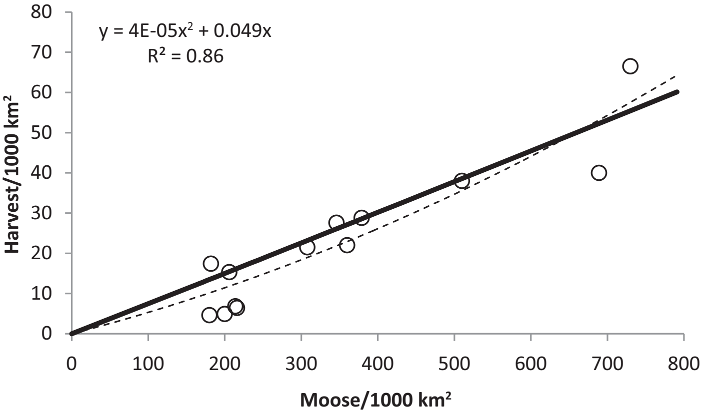

Fig. 3. Yield-density curves for moose in central British Columbia, Canada. The solid line is the modelled yield-density curve for moose in the PGSA with a harvest of 16% bulls, 2% cows and 9% calves. The open circles are the observed moose harvest and density estimates from 13 Game Management Zones in north-central British Columbia with stable moose populations (from Hatter 1999), and the dashed line is the fitted regression.

associated with both low and high SYs, wolf removal rates and moose population dynamics varied greatly within this range. The SY or yield-density curve was linear over the range in moose density (Fig. 2d), as harvest rates were constant. SYs ranged from 12 kills/1000 km^2 at 154 moose/1000 km^2 to 121 kills/1000 km^2 at 1571 moose/1000 km^2. The yield-density curve for the PGSA was similar to the preliminary yield-density curve for moose in north-central BC (Fig. 3).

Optimal harvests of bulls, cows, and calves ("fully optimized harvest rates," Table 4a), optimal bull and calf harvests with a cow harvest of 2% ("optimized bull and calf harvest rates," Table 4b), and optimal harvest of bulls in bull-only seasons ("optimized bull harvest rates," Table 4c) increased with increasing wolf removal rates. Optimized bull and calf harvest rates produced only slightly lower yields than fully optimized harvest rates. Fully optimized harvest rates and optimized bull harvest rates produced equivalent yields when wolf removal rates were low (0–10%). This was because fully optimized harvests reduced moose densities to < 200/1000 km^2 which required ≥ 50 bulls/100 cows to comply with BC's harvest management procedure, while optimized bull harvests maintained densities > 200/1000 km^2 where only ≥ 30 bulls/100 cows were required by the procedure. In all cases, the greatest harvests were achieved when adult sex ratios were maintained at the minimum bull:cow ratio objective. Calf:cow ratios were variable and reflected wolf removal rates, calf harvest rates, and density dependence.

Fully optimized harvest rates with low wolf removals (0–10%) were 6% for bulls, 0% for cows, and 28–30% for calves. With moderate to high wolf removals (20–35%), optimal harvest rates were 17–21% for bulls, 0–0.2% for cows, and 15–34% for calves. Optimal harvest rates, when wolves were absent, were 16% for bulls, 0.2% for cows, and 43% for calves. Moose harvest rates ranged from 8 to 15% and were highest when wolves were absent.

Table 4. Optimal harvest rates based on moose and wolf population parameters using wolf removal rates from 0 to 40% for the PGSA in central British Columbia, Canada.

a. Optimized harvest rates for bulls, cows and calves.

Wolf removal rate (%)	0	10	20	25	30	35	40
Wolves/1000 km^2	5	5	8	10	15	5	0
Moose/1000 km^2	120	166	363	609	1400	1400	1400
Harvest/1000 km^2	10	14	31	48	130	206	245
Bulls/100 cows	50	50	30	30	30	30	30
Calves/100 cows	26	26	31	33	38	29	24
Bull harvest rate (%)	6	6	17	18	21	18	16
Cow harvest rate (%)	0	0	0	0	0.2	0.2	0.2
Calf harvest rate (%)	30	28	19	15	15	34	43
Moose harvest rate (%)	8	8	8	7	8	13	15

b. Optimized bull and calf harvest rates with cow harvest rate = 2%.

Wolf removal rate (%)	0	10	20	25	30	35	40
Wolves/1000 km^2	4	5	8	10	15	5	0
Moose/1000 km^2	100	161	350	585	1400	1400	1400
Harvest/1000 km^2	10	13	30	46	123	200	239
Bulls/100 cows	50	50	30	30	30	30	30
Calves/100 cows	28	32	36	38	43	34	29
Bull harvest rate (%)	9	10	21	22	25	22	20
Cow harvest rate (%)	2	2	2	2	2	2	2
Calf harvest rate (%)	27	18	9	6	6	26	35
Moose harvest rate (%)	9	7	8	7	8	12	14

c. Optimized bull harvest rates with bull-only hunting.

Wolf removal rate (%)	0	10	20	25	30	35	40
Wolves/1000 km^2	9	10	13	18	16	6	0
Moose/1000 km^2	229	319	563	1040	1490	1606	1662
Harvest/1000 km^2	10	14	26	50	79	81	81
Bulls/100 cows	30	30	30	30	30	30	30
Calves/100 cows	36	37	38	39	40	34	31
Bull harvest rate (%)	19	20	20	21	22	21	20
Cow harvest rate (%)	0	0	0	0	0	0	0
Calf harvest rate (%)	0	0	0	0	0	0	0
Moose harvest rate (%)	4	4	4	5	5	5	5

DISCUSSION

I used a predator-prey model to investigate how predation may affect SYs and optimal harvest strategies for moose in central BC. I used a modified Type II functional response for wolves (Messier 1994), a ratio dependent wolf numerical response (Eberhardt 1997), and a density independent calf predation rate by bears. The modelled predator-prey parameters closely matched the observed parameters from the PGSA when the wolf removal rate was 31%. Modelled moose calf and annual mortality rates were generally consistent with Alaska and Yukon studies

(Boertje et al. 2009), and modelled wolf densities were similar to those generated from a biomass regression model. The modelled maximum rate of increase for moose ($\lambda \sim 1.3$) was similar to 1.35 estimated by Eberhardt (1997), and unhunted adult sex ratios (87–100 bulls/100 cows) were near parity as documented from published studies of naturally fluctuating moose populations (Timmermann 1992). The yield-density curve for the PGSA was comparable to the yield-density curve for moose in north-central BC (Hatter 1999) suggesting that the SY curve for the PGSA may be broadly applicable to other moose populations in BC.

Optimal harvests included a moderate harvest of bulls (16–21%), a nil-to-very low harvest of cows (0–0.2%), and moderate-to-high harvests of calves (15–43%) when wolf removal rates were ≥ 20%. These results support previous findings from Nilsen et al. (2005) and Xu and Boyce (2010) who also noted that optimal moose harvests in the presence of predators involved a high harvest of bulls and calves with a minimal cow harvest. Xu and Boyce (2010) found that harvest rates to optimize moose yields in Alberta included 40–45% of bulls, 0.1–5% of cows, and 35–40% of calves. The lower optimal harvest rates for bulls in this study were likely due to the harvest management constraints placed on adult sex ratios (i.e., ≥ 30 bulls:100 cows for > 200 moose/1000 km^2, and ≥ 50 bulls:100 cows for ≤ 200/1000 km^2).

Optimal yields of bulls and calves, with a cow harvest of 2% were only slightly lower than fully optimized yields. Some advantages of harvesting a greater proportion of cows (i.e., 2% vs. 0.2%) include an increased sample size for monitoring moose reproduction and nutritional status (Heard et al. 1997, Boertje et al. 2007), recovery of low bull:cow ratios (Young and Boertje 2008), and more options to intensify moose management at high density (Young et al. 2006). Bull-only hunting, however, may be preferable for low density moose populations limited by predation (Van Ballenberghe and Dart 1982, Environment Yukon 2016). I found that bull-only harvests with low wolf removal rates (0–10%) provided equivalent yields to selective harvests while maintaining higher moose and wolf densities.

Wolf control studies in Alaska and Yukon indicated that wolf reductions within low-density, predator-limited moose populations led to elevated moose and harvest densities followed by elevated wolf densities that equalled or exceeded pre-control levels (Gasaway et al. 1992, Boertje et al. 1996). Modelled moose densities and harvests similarly increased with intensified wolf removals due to the ratio-dependent numerical response which enabled wolf densities to increase. For example, moose densities were elevated from 207 to 1103 moose/1000 km^2, harvests from 16 to 84 moose/1000 km^2, and wolf densities from 7 to 12 wolves/1000 km^2 when wolf removal rates were increased from 10 to 30%. The modelled wolf population was able to sustain removal rates up to 31% which was consistent with Adams et al. (2008) who analysed information from 39 North American wolf populations and determined that populations were able to compensate for removal rates up to 29%.

While the predator-prey model appeared to provide a reasonable portrait of wolf-moose-bear dynamics in the PGSA from 1987 to 1998, increasing model realism would have helped to validate the model. Several studies have shown that winter kill rates by individual wolves are inversely related to pack size, and that wolf predation should be modelled by the number and size of packs (Ballard et al. 1987, McNay and Delong 1998, Hayes et al. 2000). Adams et al. (2008) discussed how wolves adjust dispersal rates as a primary mechanism to compensate for human harvest which also could be modelled. Most northern wolf-ungulate studies have identified stochastic weather events as a significant component in predator-prey systems (Gasaway et al. 1983 Gasaway et al. 1992, Boertje et al.1996, 2009, Ballard and Van Ballenberghe 1998, McNay and Delong 1998). I did not model stochastic predator-prey-weather interactions because many parameters in predator-prey models are influenced by weather which greatly increases model complexity, and because quantitative measures of imprecision (SEs) were difficult to parameterize. However, Xu and Boyce (2010) cautioned that predation and stochastic weather events can drive moose populations to low levels and negatively influence SYs.

A growing number of studies suggest ratio-dependence may be common in wolf-ungulate systems (Hebblewhite 2013). I used a ratio-dependent, wolf numerical response (Eberhardt 1997) with an equilibrium ratio of 25 moose/wolf. Studies of moose:wolf ratios during winter suggest moose densities may stabilize with 20–30 moose/wolf. Gasaway et al. (1983) summarized these studies and identified 3 general categories of moose/wolf relationships: predation was sufficient to cause a decline in moose abundance at <20 moose/wolf, appeared to control moose numbers at 20–30 moose/wolf, and was insufficient to limit growth at > 30 moose/wolf. Person et al. (2001) and Bowyer et al. (2013), however, cautioned against even a general interpretation of such ratios for interpreting impacts of wolf predation on moose.

The predator-prey model was based on moose-wolf-bear relationships in the PGSA prior to the moose population decline in the early 2000s. The decline coincided with a mountain pine beetle (*Dendroctonus ponderosae*) outbreak where habitat changes and increased salvage logging and road building may have resulted in greater vulnerability to moose from human harvest and predation, while elevating nutritional constraints and health/disease concerns (Kuzyk and Heard 2014). While disease was not considered a substantive cause of moose mortality in British Columbia from 2012 to 2019 (Kuzyk et al. 2019), it is reported as a significant mortality factor in certain North American moose populations (Murray et al. 2006). SYs appear to have been impacted from the beetle outbreak (Kuzyk et al. 2018) and optimal harvest rates may now be considerably lower than projected by the predator-prey model. Further work on anthropogenic and environmental factors affecting moose population dynamics could improve and make the model more suitable for contemporary conditions.

MANAGEMENT IMPLICATIONS AND RECOMMENDATIONS

SY curves assume that moose populations are stable, while most populations fluctuate and rarely, if ever, achieve a stable equilibrium (Sæther et al. 2001). Thus, the main value of estimating SYs was to provide an expectation of harvest under long-term, stable predator-prey interactions in central BC. The principal value of the optimal harvest calculations was to identify how various sex/age classes should be harvested under different levels of predation. Estimating SYs from the predator-prey model was limited by the lack of data on First Nations harvest, calf vulnerability to predation during summer, and uncertainty in the wolf functional and numerical responses. Nonetheless, the model findings that moose harvests should consist primarily of bulls and calves with nil to very low cow harvests was consistent with other published studies, and suggest these findings are broadly applicable to moose-wolf-bear systems where alternate prey are rare.

Managers who wish to elevate cow harvests in order to monitor moose reproduction and nutritional status, or to recover low bull:cow ratios, should reduce calf harvests to compensate for the increased harvest of cows. Further restrictions such as bull-only harvests should be considered for low-density, predator-limited moose populations. When moose populations are food-limited, harvests of bulls, cows, and calves should be elevated to maintain populations below *K* and enhance yields. Finally, and most importantly, moose harvests should be set below optimal yields to account for stochastic variation in predator-prey interactions, changing environmental conditions, and management uncertainty.

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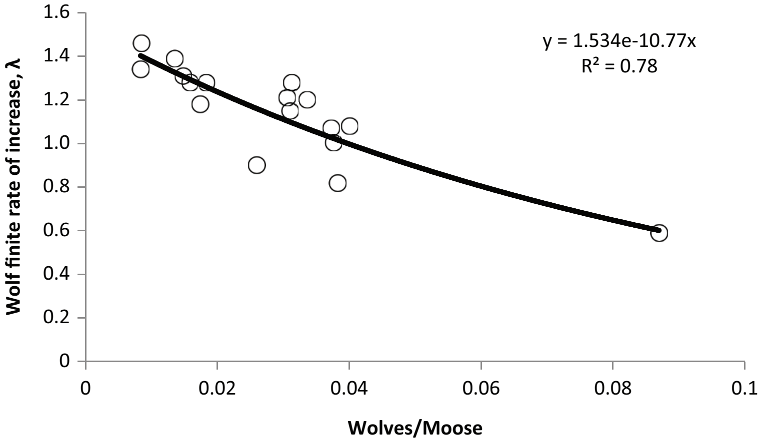
Appendix 1. Relationship between wolf finite rate of increase (λ) and the wolves:moose ratio from 17 North American wolf populations.



Location	Wolves/moose[1]	Wolf λ	Reference
Alaska	0.0083	1.340	Keith 1983
Alberta	0.0085	1.460	Keith 1983
Michigan	0.0135	1.390	Keith 1983
Minnesota	0.0148	1.310	Keith 1983
Denali Park	0.0159	1.280	McNay and Delong 1998[2]
Kenai, Alaska	0.0174	1.180	Eberhardt and Peterson 1999
Interior Alaska	0.0183	1.280	McNay and Delong 1998[2]
Denali Park	0.0260	0.900	McNay and Delong 1998[2]
Alberta	0.0306	1.210	Keith 1983
Michigan	0.0310	1.150	Keith 1983
Nelchina, Alaska	0.0313	1.280	Eberhardt and Peterson 1999
Ontario	0.0336	1.200	Keith 1983
NC Minnesota	0.0373	1.070	Eberhardt and Peterson 1999
Isle Royale	0.0376	1.004	https://isleroyalewolf.org/[2]
Isle Royale	0.0382	0.820	McNay and Delong 1998[2]
Quebec	0.0400	1.080	Eberhardt and Peterson 1999
Interior Alaska	0.0870	0.590	McNay and Delong 1998[2]

[1] wolves per moose biomass equivalent (Keith 1983).
[2] additional data used in this study to estimate the wolves:moose equilibrium ratio.